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THE ECOLOGY OF THE MANGROVES OF SOUTH FLORIDA: A COMMUNITY PROFILE

by

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CHAPTER 1. INTRODUCTION

1.1 "MANGROVE" DEFINITION

The term "mangrove" expresses two distinctly different concepts. One usage refers to halophytic species of trees and shrubs (halophyte = plant growing in saline soil). In this sense, mangrove is a catch-all, botanically diverse, non-taxonomic expression given to approximately 12 families and more than 50 species (Chapman 1970) of tropical trees and shrubs (see Waisel 1972 for a detailed list). While not necessarily closely related, all these plants are adapted to (1) loose, wet soils, (2) a saline habitat, (3) periodic tidal submergence, and (4) usually have degrees of viviparity of propagules (see section 2.3 for discussion of "viviparity" and "propagules").

The second usage of the term mangrove encompasses the entire plant community including individual mangrove species. Synonymous terms include tidal forest, tidal swamp forest, mangrove community, mangrove ecosystem, mangal (Macnae 1968), and mangrove swamp.

For consistency, in this publication we will use the word "mangrove" for individual kinds of trees; mangrove community, mangrove ecosystem or mangrove forest will represent the entire assemblage of "mangroves".

1.2 FACTORS CONTROLLING MANGROVE DISTRIBUTION

Four major factors appear to limit the distribution of mangroves and determine the extent of mangrove ecosystem development. These factors include (1) climate, (2) salt water, (3) tidal fluctuation, and (4) substrate.

Climate

Mangroves are tropical species and do not develop satisfactorily in regions where the annual average temperature is below 19°C or 66°F (Waisel 1972). Normally, they do not tolerate temperature fluctuations exceeding 10°C (18°F) or temperatures below freezing for any length of time. Certain species, for example, black mangrove, *Avicennia germinans*, on the northern coast of the Gulf of Mexico, maintain a semi-permanent shrub form by growing back from the roots after freeze damage.

Lugo and Zucca (1977) discuss the impact of low temperature stress on Florida mangroves. They found that mangrove communities respond to temperature stress by decreasing structural complexity (decreased tree height, decreased leaf area index, decreased leaf size, and increased tree density). They concluded that mangroves growing under conditions of high soil salinity stress are less tolerant of low temperatures. Presumably, other types of stress (e.g., pollutants, diking) could reduce the temperature tolerance of mangroves.

High water temperatures can also be limiting. McMillan (1971) reported that seedlings of black mangrove were killed by temperatures of 39° to 40°C (102° to 104°F) although established seedlings and trees were not damaged. To our knowledge, upper temperature tolerances for adult mangroves are not well known. We suspect that water temperatures in the range 42° to 45°C (107° to 113°F) may be limiting.

Salt Water

Mangroves are facultative halophytes, i.e., salt water is not a physical requirement (Bowman 1917; Egler 1948). In fact, most mangroves are capable of growing quite well in freshwater (Teas 1979). It is important to note, however, that mangrove ecosystems do not develop in strictly freshwater environments; salinity is important in reducing competition from other vascular plant species (Kuenzler 1974). See section 2.2 about salinity tolerance of mangrove species.

Tidal Fluctuation

While tidal influence is not a direct physiological requirement for mangroves, it plays an important indirect role. First, tidal stress (alternate wetting and drying), in combination with salinity, helps exclude most other vascular plants and thus reduces competition. Second, in certain locations, tides bring salt water up the estuary against the outward flow of freshwater and allow mangroves to become established well inland. Third, tides may transport nutrients and relatively clean water into mangrove ecosystems and export accumulations of organic carbon and reduced sulfur compounds. Fourth, in areas with high evaporation rates, the action of the tides helps to prevent soil salinities from reaching concentrations which might be lethal to mangroves. Fifth, tides aid in the dispersal of mangrove propagules and detritus.

Because of all of these factors, termed tidal subsidies by E.P. Odum (1971), mangrove ecosystems tend to reach their greatest development around the world in low-lying regions with relatively large tidal ranges. Other types of water fluctuation, e.g., seasonal variation in freshwater runoff from the Florida Everglades, can provide similar subsidies.

Substrate and Wave Energy

Mangroves grow best in depositional environments with low wave energy. High wave energy prevents establishment of propagules, destroys the relatively shallow mangrove root system and prevents the accumulation of fine sediments. The most productive mangrove ecosystems develop along deltaic coasts or in estuaries that have fine-grained muds composed of silt, clay and a high percentage of organic matter. Anaerobic sediments pose no problems for mangroves (see section 2.1) and exclude competing vascular plant species.

1.3 GEOGRAPHICAL DISTRIBUTION

Mangroves dominate approximately 75% of the world's tropical coastline between 25°N and 25°S latitude (McGill 1959). On the east coast of Africa, in Australia and in New Zealand, they extend 10° to 15° farther south (Kuenzler 1974) and in Japan, Florida, Bermuda, and the Red Sea they extend 5° to 7° farther north. These areas of extended range generally occur where oceanographic conditions move unusually warm water away from the equator.

Although certain regions such as the tropical Indo-Pacific have as many as 30 to 40 species of mangroves present, only three species are found in Florida: the red mangrove, <u>Rhizophora mangle</u>, the black mangrove, <u>Avicennia germinans</u>, and the white mangrove, <u>Laguncularia racemosa</u>. A fourth species, buttonwood, <u>Conocarpus erecta</u>, is not a true mangrove (no tendency to vivipary or root modification), but is an important species in the transition zone on the upland edge of mangrove ecosystems (Tomlinson 1980).

The ranges of mangrove species in Florida have fluctuated over the past several centuries in response to relatively short-term climatic change. Currently, the situation is as follows (Figure 1). The red mangrove and the white mangrove have been reported as far north as Cedar Key on the west coast of Florida (Rehm 1976) and north of the Ponce de Leon Inlet on the east coast (Teas 1977); both of these extremes lie at approximately $29^{\circ}10'$ N latitude. Significant stands lie south of Cape Canaveral on the east coast and Tarpon Springs on the west coast. The black mangrove has been reported as far north as 30°N latitude on the east coast of Florida (Savage 1972) and as scattered shrubs along the north coast of the Gulf of Mexico.

Intertidal Distribution

The generalized distribution of the red and black mangrove in relation to the intertidal zone is shown in Figure 2a. Local variations and exceptions to this pattern occur commonly in response to localized differences in substrate type and elevation, rates of sea level rise, and a variety of other factors (see section 3.2 for a full discussion of mangrove

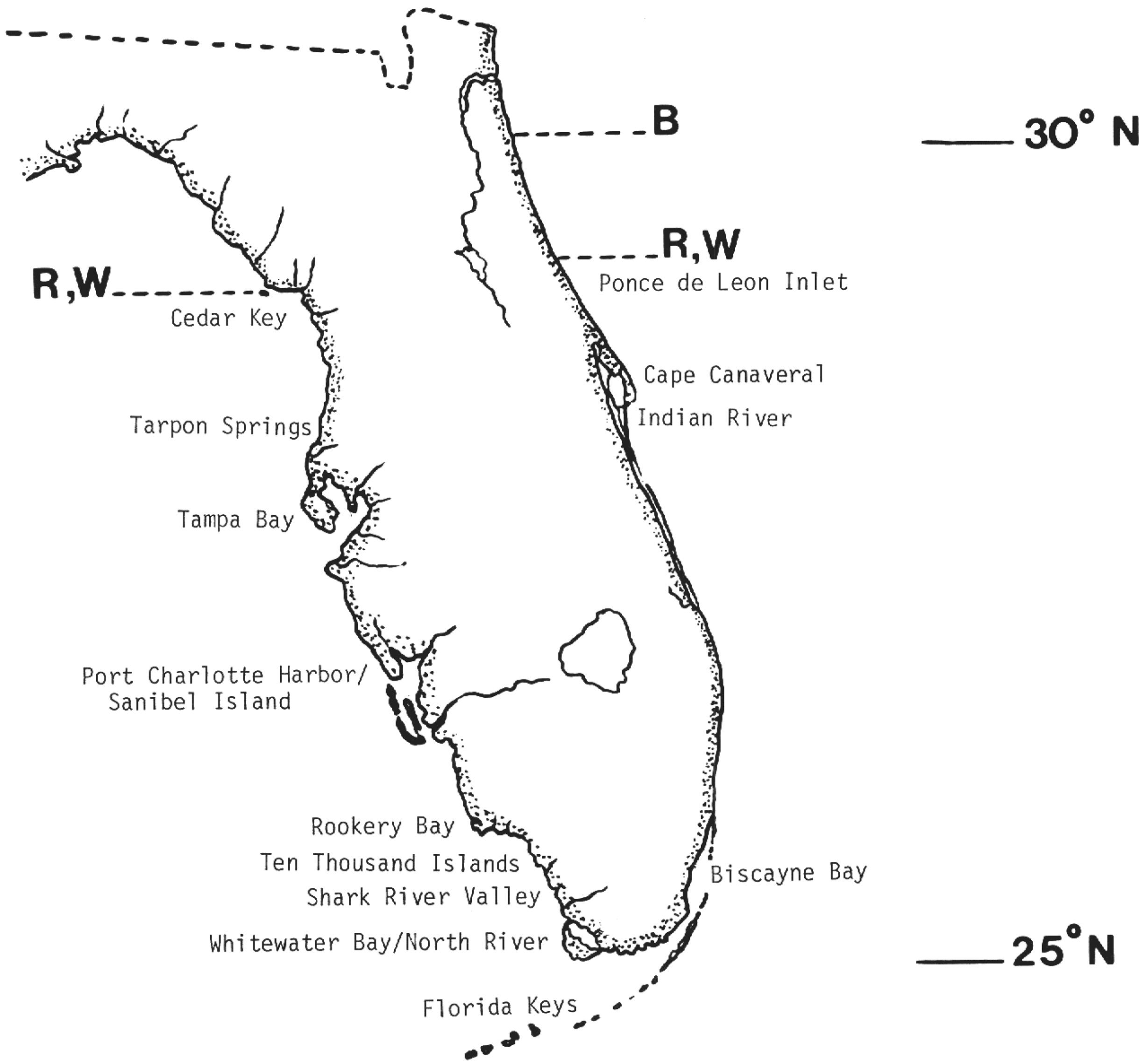
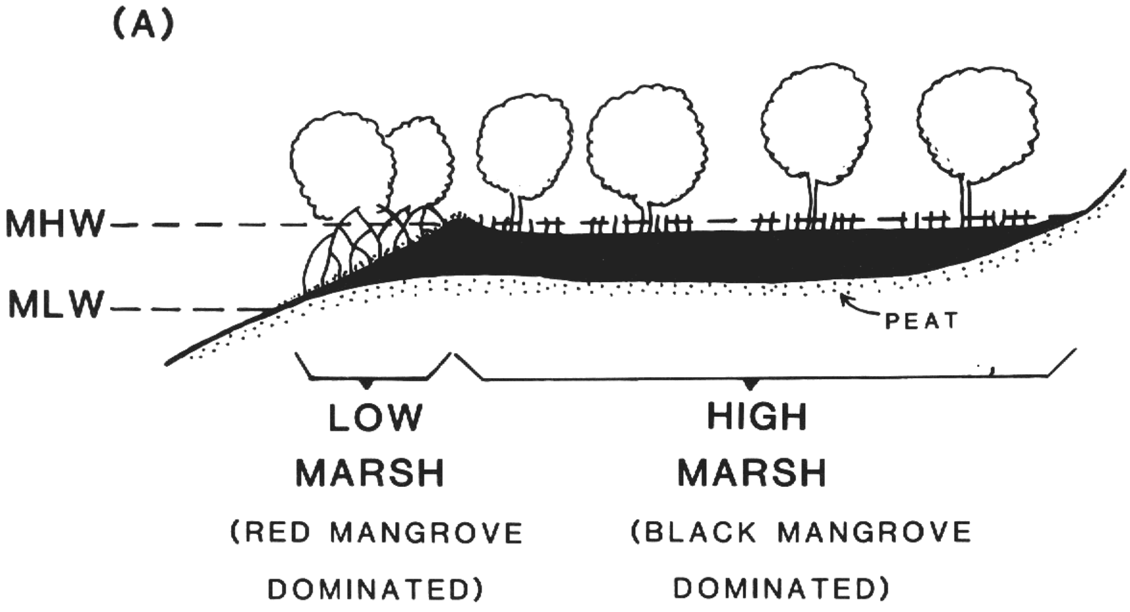


Figure 1. Approximate northern limits for the red mangrove (R), black mangrove (B), and white mangrove (W) in Florida (based on Savage 1972); although not indicated in the figure, the black mangrove extends along the northern Gulf of Mexico as scattered shrubs.



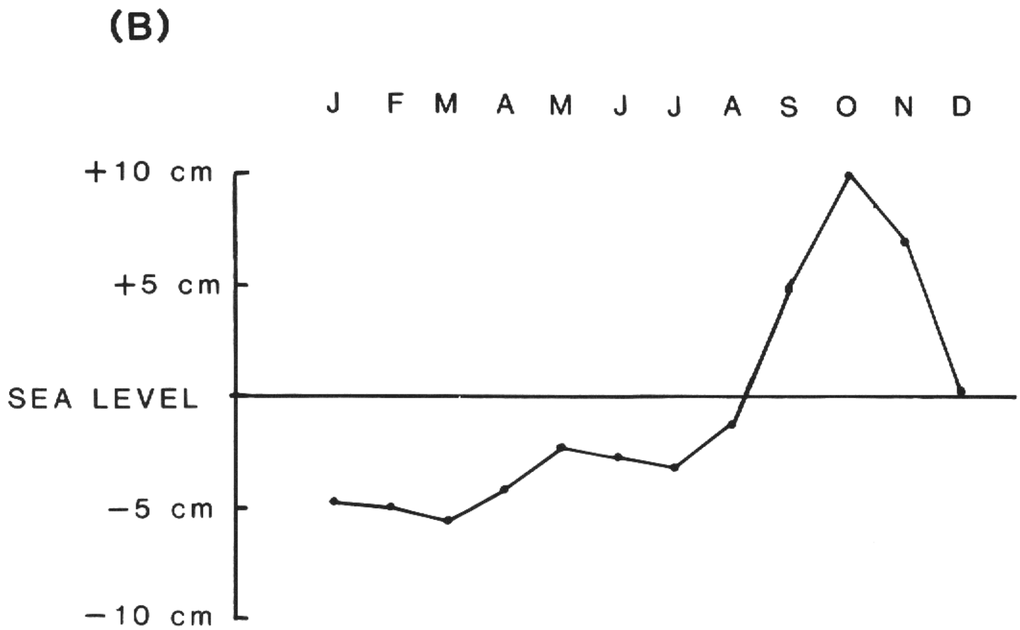


Figure 2. (a) A typical intertidal profile from south Florida showing the distribution of red and black mangrove (adapted from Provost 1974). (b) The pattern of annual sea level change in south Florida (Miami)(adapted from Provost 1974).

zonation). Furthermore, it is important to recognize that the intertidal zone in most parts of Florida changes seasonally (Provost 1974); there is a tendency for sea level to be higher in the fall than in the spring (Figure 2b). As a result the "high marsh" may remain totally dry during the spring and be continually submerged in the autumn. This phenomenon further complicates the textbook concept of the intertidal, "low marsh" red mangrove and the infrequently flooded, "high marsh" black mangrove.

Mangrove Acreage in Florida

Estimates of the total acreage occupied by mangrove communities in Florida vary widely between 430,000 acres and over 500,000 acres (174,000 ha to over 202,000 ha). Eric Heald (Tropical Bioindustries, 9869 Fern St., Miami, Fla.; personal communication 1981) has identified several reasons for the lack of agreement between estimates. These include: (1) inclusion or exclusion in surveys of small bays, ponds and creeks which occur within mangrove forests, (2) incorrect identification of mangrove areas from aerial photography as a result of inadequate "ground-truth" observations, poorly controlled aerial photography, and simple errors of planimetry caused by photography of inadequate scale.

The two most detailed estimates of area covered by mangroves in Florida are provided by the Coastal Coordinating Council, State of Florida (1974) and Birnhak and Crowder (1974). Considerable differences exist between the two estimates. The estimate of Birnhak and Crowder (1974), which is limited to certain areas of south Florida, appears to be unrealistically high, particularly for Monroe County (Eric Heald, personal communication 1981). Coastal Coordinating Council (1974) estimates a total of 469,000 acres (190,000 ha) within the State and suggests an expected margin of error of 15% (i.e. their estimate lies between 400,000 and 540,000 acres or 162,000 and 219,000 ha). According to this survey, ninety percent of Florida's mangroves are located in the four southern counties of Lee (35,000 acres or 14,000 ha), Collier (72,000 acres or 29,000 ha), Monroe (234,000 acres or 95,000 ha), and Dade (81,000 acres or 33,000 ha).

Much of the area covered by mangroves in Florida is presently owned by Federal, State or County governments, or by non-profit organizations such as the National Audubon Society. Approximately 280,000 acres (113,000 ha) fall into this category (Eric Heald, personal communication 1981). Most of this acreage is held by the Federal Government as a result of the land being including within the Everglades National Park.

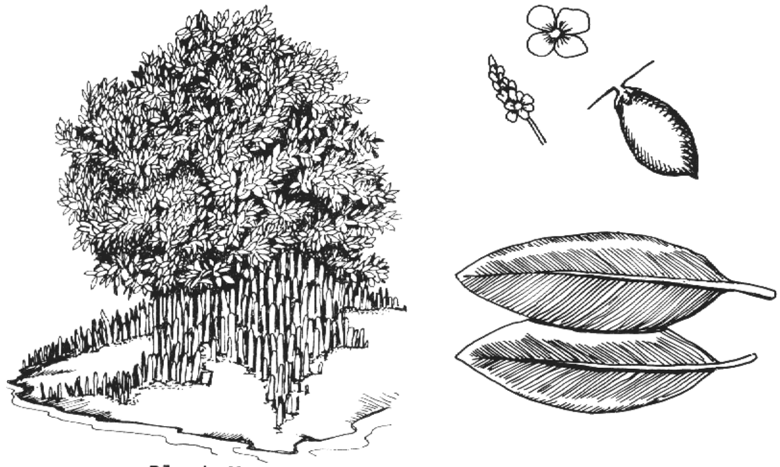
1.4 MANGROVE SPECIES DESCRIPTIONS

The following descriptions come largely from Carlton (1975) and Savage (1972); see these publications for further comments and photographs. For more detailed descriptions of germinating seeds (propagules) see section 2.3. The three species are shown in Figure 3.

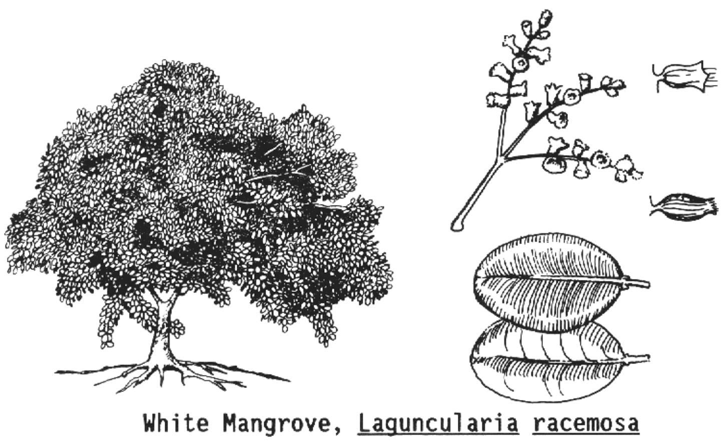
The Black Mangrove (*Avicennia germinans*)

Avicennia germinans is synonymous with *A. nitida* and is a member of the family Avicenniaceae (formerly classed under Verbenaceae). The tree may reach a height of 20 m (64 ft) and has dark, scaly bark. Leaves are 5 to 10 cm (2 to 4 inches) in length, narrowly elliptic or oblong, shiny green above and covered with short, dense hairs below. The leaves are frequently encrusted with salt. This tree is characterized by long horizontal or "cable" roots with short vertical aerating branches (pneumatophores) that profusely penetrate the substrate below the tree. Propagules are lima-bean shaped, dark green while on the tree, and several centimeters (1 inch) long. The tree flowers in spring and early summer.

Red Mangrove, Rhizophora mangle



Black Mangrove, Avicennia germinans



White Mangrove, Laguncularia racemosa

Figure 3. Three species of Florida mangroves with propagules, flowers, and leaves.

The White Mangrove (*Laguncularia racemosa*)

The white mangrove is one of 450 species of plants in 18 genera of the family Combretaceae (synonymous with Terminaliaceae). It is a tree or shrub reaching 15 m (49 ft) or more in height with broad, flattened oval leaves up to 7 cm (3 inches) long and rounded at both ends. There are two salt glands at the apex of the petiole. The propagule is very small (1.0 to 1.5 cm or 0.4 to 0.6 inches long) and broadest at its apex. Flowering occurs in spring and early summer.

The Red Mangrove (*Rhizophora mangle*)

The red mangrove is one of more than 70 species in 17 genera in the family Rhizophoraceae. This tree may reach 25 m (80 ft) in height, has thin grey bark and dark red wood. Leaves may be 2 to 12 cm (1 to 5 inches) long, broad and blunt-pointed at the apex. The leaves are shiny, deep green above and paler below. It is easily identified by its characteristic "prop roots" arising from the trunk and branches. The pencil-shaped propagules are as much as 25 to 30 cm (10 to 12 inches) long after germination. It may flower throughout the year, but in Florida flowering occurs predominately in the spring and early summer.

1.5 MANGROVE COMMUNITY TYPES

Mangrove forest communities exhibit tremendous variation in form. For example, a mixed scrub forest of black and red mangroves at Turkey Point on Biscayne Bay bears little resemblance to the luxuriant forests, dominated by the same two species, along the lower Shark River.

Lugo and Snedaker (1974) provided a convenient classification system based on mangrove forest physiogomy. They identified six major community types resulting from different geological and hydrological processes. Each type has its own characteristic set of environmental variables such as soil type and depth, soil salinity range, and flushing rates. Each community type has characteristic ranges of primary production, litter decomposition and carbon export along with differences in nutrient recycling rates, and community components. The community types as shown in Figure 4 are as follows:

(1) Overwash mangrove forests - these islands are frequently overwashed by tides and thus have high rates of organic export. All species of mangroves may be present, but red mangroves usually dominate. Maximum height of the mangroves is about 7 m (23 ft).

(2) Fringe mangrove forests - mangroves form a relatively thin fringe along waterways. Zonation is typically as described by Davis (1940) (see discussion in section 3.2). These forests are best defined along shorelines whose elevations are higher than mean high tide. Maximum height of the mangroves is about 10 m (32 ft).

(3) Riverine mangrove forests - this community type includes the tall flood plain forests along flowing waters such as tidal rivers and creeks. Although a shallow berm often exists along the creek bank, the entire forest is usually flushed by daily tides. All three species of mangroves are present, but red mangroves (with noticeably few, short prop roots) predominate. Mangroves may reach heights of 18 to 20 m (60 to 65 ft).

(4) Basin mangrove forests - these forests occur inland in depressions channeling terrestrial runoff toward the coast. Close to the coast they are influenced by daily tides and are usually dominated by red mangroves. Moving inland, the tidal influence lessens and dominance shifts to black and white mangroves. Trees may reach 15 m (49 ft) in height.

(5) Hammock forests - hammock mangrove communities are similar to the basin type except that they occur on ground that is slightly elevated (5 to 10 cm or 2 to 4 inches) relative to surrounding areas.

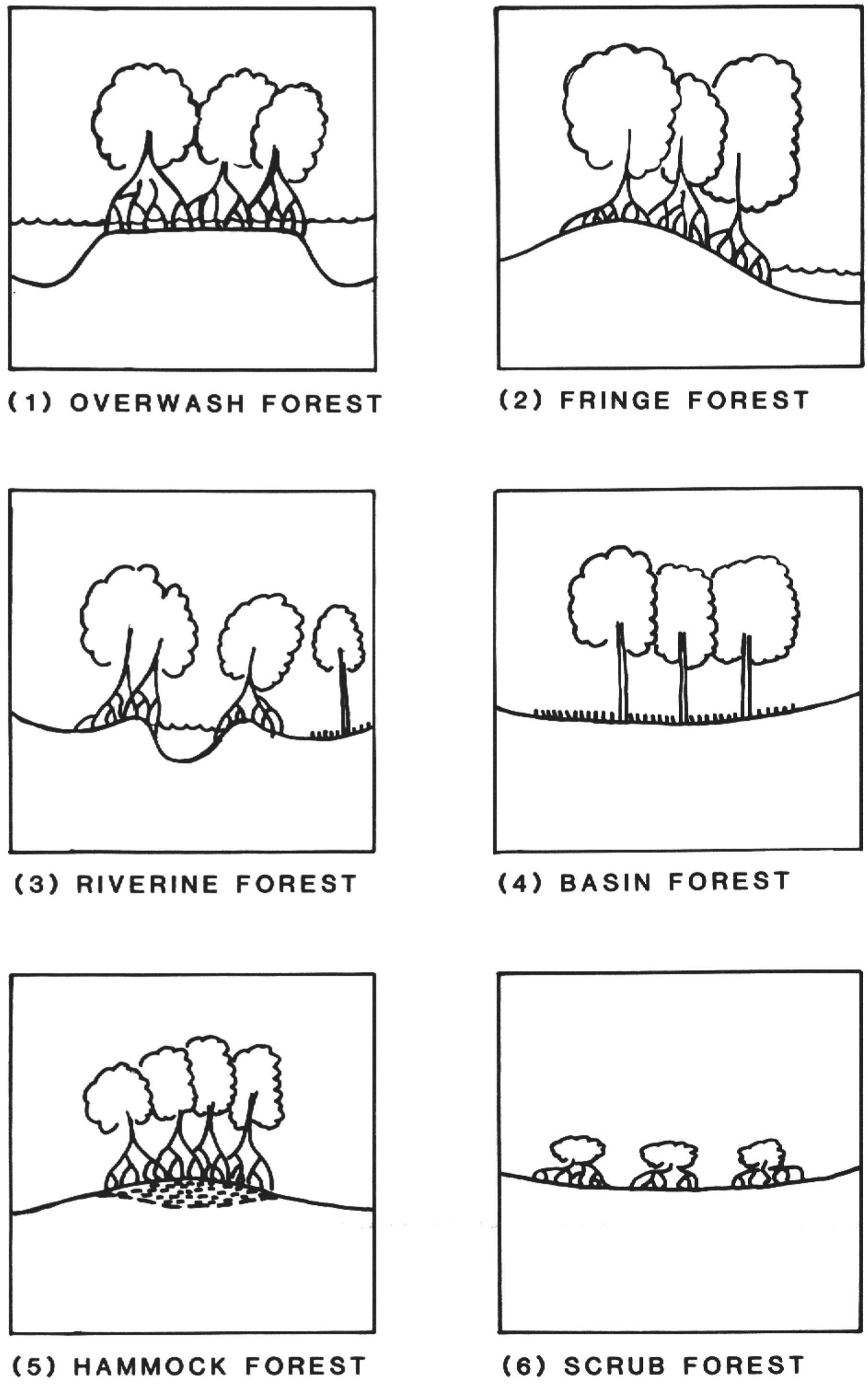


Figure 4. The six mangrove community types (Lugo and Snedaker 1974).

All species of mangroves may be present. Trees rarely exceed 5 m (16 ft) in height.

(6) Scrub or dwarf forests - this community type is limited to the flat coastal fringe of south Florida and the Florida Keys. All three species are present. Individual plants rarely exceed 1.5 m (4.9 ft) in height, except where they grow over depressions filled with mangrove peat. Many of these tiny trees are 40 or more years of age. Nutrients appear to be limiting although substrate (usually limestone marl) must play a role.

Throughout this publication we have attempted to refer to Lugo and Snedaker's classification scheme wherever possible. Without a system of this type, comparisons between sites become virtually meaningless.

1.6 SUBSTRATES

Understanding mangrove-substrate relationships is complicated by the ability of mangroves to grow on many types of substrates and because they often alter the substrate through peat formation and by altering patterns of sedimentation. As a result, mangroves are found on a wide variety of substrates including fine, inorganic muds, muds with a high organic content, peat, sand, and even rock and dead coral if there are sufficient crevices for root attachment. Mangrove ecosystems, however, appear to flourish only on muds and fine-grained sands.

In Florida, the primary mangrove soils are either calcareous marl muds or calcareous sands in the southern part of the State and siliceous sands farther north (Kuenzler 1974). Sediment distribution and, hence, mangrove development, is controlled to a considerable extent by wave and current energy. Low energy shorelines accumulate fine-grained sediments such as mud and silt and usually have the best mangrove growth. Higher energy shorelines (more wave action or higher current velocities) are characterized by sandy sediments and less productive mangroves. If the wave energy becomes too great, mangroves will not be present. Of the three species of Florida mangroves, white mangroves appear to tolerate sandy substrates the best (personal observation), possibly because this species may tolerate a greater depth to the water table than the other two species.

Mangroves in Florida often modify the underlying substrate through peat deposition. It is not unusual to find layers of mangrove peat several meters thick underlying well-established mangrove ecosystems such as those along the southwest coast of Florida. Cohen and Spackman (1974) presented a detailed account of peat formation within the various mangrove zones of south Florida and also in areas dominated by black needle rush (Juncus roemerianus), smooth cordgrass (Spartina alterniflora) and a variety of other macrophytes; Cohen and Spackman (1974) also provide descriptions and photography to aid in the identification of unknown peat samples.

The following descriptions come from Cohen and Spackman (1974) and from the personal observations of W.E. Odum and E.J. Heald. Red mangroves produce the most easily recognized peat. More recent deposits are spongy, fibrous and composed to a great extent of fine rootlets (0.2 to 3.0 mm in diameter). Also present are larger pieces of roots (3 to 25 mm), bits of wood and leaves, and inorganic materials such as pyrite, carbonate minerals, and quartz. Older deposits are less easily differentiated although they remain somewhat fibrous. Peat which has recently been excavated is reddish-brown although this changes to brown-black after a short exposure to air. Older deposits are mottled reddish-brown; deposits with a high content of carbonates are greyish-brown upon excavation.

Cohen and Spackman (1974) were unable to find deposits of pure black mangrove or white mangrove peat suggesting that these two species may not form extensive deposits of peat while growing in pure stands. There are, however, many examples of peats which are mixtures of red mangrove material and black mangrove roots. They suggested that the black mangrove peats identified by Davis (1946) were probably mixtures of peat from several sources.

Throughout south Florida the substrate underlying mangrove forests may consist of complicated patterns of calcareous muds, marls, shell, and sand interspersed and overlain by layers of mangrove peat and with limestone bedrock at the bottom. Detailed descriptions of this complex matrix and its spatial variation were given by Davis (1940, 1943, 1946), Egler (1952), Craighead (1964), Zieman (1972) and Cohen and Spackman (1974) among others. Scoffin (1970) discussed the ability of red mangrove to trap and hold sediments about its prop roots. So called "land-building" by mangroves is discussed in section 3.2.

The long-term effect of mangrove peat on mangrove distribution is not entirely clear. Certainly, if there is no change in sea level or if erosion is limited, the accumulation of peat under stands of red mangroves combined with deposition and accumulation of suspended sediments will raise the forest floor sufficiently to lead to domination by black or white mangroves and, ultimately, more terrestrial species. Whether this is a common sequence of events in contemporary south Florida is not clear. It is clear that peat formtion is a passive process and occurs primarily where and when physical processes such as erosion and sea level rise are of minimal importance (Wanless 1974).

Zieman (1972) presented an interesting argument suggesting that mangrove peat may be capable of dissolving underlying limestone rock, since carbonates may dissolve at pH 7.8. Through this process, shallow depressions might become deeper and the overlying peat layer thicker without raising the surface of the forest floor.

Data on chemical characteristics of Florida mangrove soils and peat are limited. Most investigators have found mangrove substrates to be almost totally anaerobic. Lee (1969) recorded typical Eh values of -100 to -400 mv in mangrove peats. Such evidence of strongly reducing conditions are not surprising considering the fine-grained, high organic nature of most mangrove sediments. Although mangroves occur in low organic sediments (less than 1% organic matter), typical values for mangrove sediments are 10% to 20% organic matter.

Lee (1969) analyzed 3,000- to 3,500-year-old mangrove peat layers underlying Little Black Water Sound in Florida Bay for lipid carbon content. Peat lipid content varied between 0.6 and 2.7 mg lipid-C/gram of peat (dry wt) or about 3% of the total organic carbon total. These values usually increased with depth. Long chain fatty acids (C-16 and C-18) were the dominant fatty acids found.

Florida mangrove peats are usually acidic, although the presence of carbonate materials can raise the pH above 7.0. Zieman (1972) found red mangrove peats to range from pH 4.9 to 6.8; the most acid conditions were usually found in the center of the peat layer. Lee (1969) recorded a pH range from 5.8 to 6.8 in red mangrove peat at the bottom of a shallow embayment. Although Davis (1940) found a difference between red mangrove peat (5.0 to 5.5) and black mangrove peat (6.9 to 7.2), this observation has not been confirmed because of the previously mentioned difficulty in finding pure black mangrove peat.

Presumably, the acidic character of mangrove peat results from release of organic acids during anaerobic decomposition and from the oxidation of reduced sulfur compounds if the peat is dried in the presence of oxygen. This last point explains why "reclaimed" mangrove areas often develop highly acidic soils (pH 3.5 to 5.0) shortly after reclamation. This "cat clay" problem has greatly complicated the conversion of mangrove regions to agricultural land in Africa and southeast Asia (Hesse 1961; Hart 1962, 1963; Macnae 1968).

In summary, although current understanding of mangrove peats and soils is fragmentary and often contradictory, we can outline several generalizations:

(1) Mangroves can grow on a wide variety of substrates including mud, sand, rock, and peat.

(2) Mangrove ecosystems appear to flourish on fine-grained sediments which are usually anaerobic and may have a high organic content.

(3) Mangrove ecosystems which persist for some time may modify the underlying substrate through peat formation. This appears to occur only in the absence of strong physical forces.

(4) Mangrove peat is formed primarily by red mangroves and consists predominantly of root material.

(5) Red mangrove peats may reach thicknesses of several meters, have a relatively low pH, and may be capable of dissolving underlying layers of limestone.

(6) When drained, dried, and aerated, mangrove soils usually experience dramatic increases in acidity due to the oxidation of reduced sulfur compounds. This greatly complicates their conversion to agriculture.

1.7 WATER QUALITY

Water quality characteristics of surface waters flowing through Florida mangrove ecosystems exhibit great variation from one location to the next. Proximity to terrestrial ecosystems, the ocean, and human activities are all important in determining overall water quality. Equally important is the extent of the mangrove ecosystem since drastic alterations in water quality can occur within a stand of mangroves.

In general, the surface waters associated with mangroves are characterized by (1) a wide range of salinities from virtually fresh water to above 40 ppt (discussed in section 2.2), (2) low macronutrient concentrations (particularly phosphorous), (3) relatively low dissolved oxygen concentrations, and (4) frequently increased water color and turbidity. The last three characteristics are most pronounced in extensive mangrove ecosystems such as those adjacent to the Everglades and least pronounced in small, scattered forests such as the overwash islands in the Florida Keys.

Walsh (1967), working in a mangrove swamp in Hawaii, was one of the first to document the tendency of mangrove ecosystems to act as a consumer of oxygen and a sink for nutrients such as nitrogen and phosphorous. Carter et al. (1973) and Lugo et al. (1976) confirmed these observations for Florida mangrove swamps. Evidently, nutrients are removed and oxygen consumed by a combination of periphyton on mangrove prop roots, mud, organic detritus on the sediment surface, the fine root system of the mangroves, small invertebrates, benthic and epiphytic algae, and bacteria and fungi on all these surfaces.

The results of oxygen depletion and nutrient removal are (1) dissolved oxygen concentrations below saturation, typically 2 to 4 ppm and often near zero in stagnant locations and after heavy, storm-generated runoff, (2) very low total phosphorus values, frequently below detection limits, and (3) moderate total nitrogen values (0.5 to 1.5 mg/l). In addition, TOC (total organic carbon) may range from 4 to 50 ppm or even higher after rain; Eric Heald (personal communication 1981) has measured DOC (dissolved organic carbon) values as high as 110 ppm in water flowing from mangroves to adjacent bays. Turbidity usually falls in the 1 to 15 JTU (Jackson turbity units) range. The pH of the water column in Florida swamps is usually between 6.5 and 8.0 and alkalinity between 100 to 300 mg/l. Obviously, exceptions to all of these trends can occur. Both natural and human disturbance can raise macronutrient levels markedly.